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Alternative states of a semiarid grassland ecosystem: implications for ecosystem services

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Abstract. Ecosystems can shift between alternative states characterized by persistent differences in structure, function, and capacity to provide ecosystem services valued by society. We examined empirical evidence for alternative states in a semiarid grassland ecosystem where topographic complexity and contrasting management regimes have led to spatial variations in levels of livestock grazing. Using an inventory data set, we found that plots ($n = 72$) cluster into three groups corresponding to generalized alternative states identified in an a priori conceptual model. One cluster (*biocrust*) is notable for high coverage of a biological soil crust functional group in addition to vascular plants. Another (*grass-bare*) lacks biological crust but retains perennial grasses at levels similar to the *biocrust* cluster. A third (*annualized-bare*) is dominated by invasive annual plants. Occurrence of *grass-bare* and *annualized-bare* conditions in areas where livestock have been excluded for over 30 years demonstrates the persistence of these states. Significant differences among all three clusters were found for percent bare ground, percent total live cover, and functional group richness. Using data for vegetation structure and soil erodibility, we also found large among-cluster differences in average levels of dust emissions predicted by a wind-erosion model. Predicted emissions were highest for the *annualized-bare* cluster and lowest for the *biocrust* cluster, which was characterized by zero or minimal emissions even under conditions of extreme wind. Results illustrate potential trade-offs among ecosystem services including livestock production, soil retention, carbon storage, and biodiversity conservation. Improved understanding of these trade-offs may assist ecosystem managers when evaluating alternative management strategies.

Key words: biological soil crusts; *Bromus tectorum*; Colorado Plateau; drylands; dust; ecosystem services; functional groups; livestock grazing; resilience; state and transition model; wind erosion.

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INTRODUCTION

Ecosystems can shift between alternative states or dynamic regimes that are characterized by persistent differences in structure and function (Beisner et al. 2003, Scheffer and Carpenter 2003, Mayer and Rietkerk 2004). Such shifts are caused by factors that independently or interactively trigger relatively major changes in functional group structure, disturbance regimes, and/or

resource regimes (Chapin et al. 1996). In the context of ecosystem management, alternative states are of concern for two primary reasons. First, shifts between alternative states may occur as relatively abrupt, nonlinear responses to factors such as climate and human land use (Scheffer and Carpenter 2003, Briske 2006). The potential for abrupt changes in ecosystem properties generates a high degree of uncertainty and unpredictability in management (Holling 1996). Second, alternative states invariably differ from one another in their capacity to provide ecosystem services and support different management objectives. Once a state shift has occurred, restoration of previous conditions and management options may be difficult, costly, or effectively impossible (Whisenant 1999, Suding and Hobbs 2009).

Two major research themes have developed around the phenomenon of alternative ecosystem states. The first has focused on biotic and abiotic attributes that confer resilience to perturbations and thus, reduce ecosystem susceptibility to state shifts (Walker 1992, Carpenter et al. 2001). Resilience, defined as the magnitude of perturbation that a system can withstand while maintaining its fundamental structure and function (Holling 1996), is a dynamic property that can change in response to human impacts or climatic conditions (Scheffer and Carpenter 2003). Resilience has become a central concept for work on ecosystem sustainability in the context of global climate change and increasing human pressures on the environment (Chapin et al. 2009). The second theme has focused on thresholds between alternative states, often with an emphasis on predicting thresholds to inform ecosystem management (Westoby et al. 1989, Bestelmeyer 2006, Briske 2006). Challenges in the identification and prediction of threshold behaviors have led to questions regarding the practical applicability of the threshold concept to ecosystem management (Groffman et al. 2006). These same challenges have led to recommendations for greater management emphasis on maintaining resilience of ecosystem states that provide the broadest and most valued range of ecosystem services rather than focusing efforts on the identification of thresholds (Briske et al. 2008).

Alternative states have been described for many types of ecosystems (Folke et al. 2004, Mayer and Rietkerk 2004), but drylands are among the most susceptible to this phenomenon due to low and variable amounts of precipitation in combination with effects of human land-use activities (Schlesinger et al. 1990, van de Koppel et al. 1997, Reynolds et al. 2007). Published examples of alternative states in drylands represent variations on three common syndromes (Okin et al. 2009). The first is characterized by a persistent increase in the ratio of woody plants to perennial grasses, with woody plant dominance reinforced by feedbacks involving decreased fire frequency and/or the loss or redistribution of soil resources (Schlesinger et al. 1990, Archer et al. 1995). The second is characterized by a persistent shift in dominance from perennial plants to invasive annual plants (especially grasses), often accompanied by a feedback with increased fire frequency (D'Antonio and Vitousek 1992). The third is reflected by feedbacks between soil degradation and a persistent decline in total vegetative cover (van de Koppel et al. 1997).

We examine evidence for the existence of alternative states in a semiarid grassland ecosystem on the Colorado Plateau, USA, where livestock grazing, climate, and invasive annual plants have contributed to persistent changes in ecosystem properties. This ecosystem is characterized by the presence of biological soil crusts (biological crust, hereafter), which are soil-surface assemblages of cyanobacteria, mosses, and lichens that are functionally significant for soil stabilization (Belnap 1995, Warren 2003), nutrient cycling (Evans and Lange 2003), hydrologic processes (Eldridge et al. 2002, Warren 2003), and mediation of vascular plant establishment (Belnap et al. 2003, Escudero et al. 2007). The functional significance of biological crust is countered by its high vulnerability to surface disturbances that can result in long-term reductions of crust structure and functionality (Belnap and Eldridge 2003). In sparsely vegetated drylands, disturbance-induced declines in biological crust often are accompanied by accelerated soil erosion and persistent changes in soil physical and biogeochemical properties (Neff et al. 2005). Dust emitted from unstable drylands also can have downwind impacts on air quality and human health, ecosystem biogeochemistry (Neff et al. 2008), and regional-scale hydrologic processes (Painter et al. 2010). Our objectives were to

(1) validate our a priori conception of possible alternative states using empirical field data collected across a range of conditions and land uses; (2) evaluate the functional outcome of state changes, focusing on modeled potential wind erosion; (3) relate our results to principles of resilience theory; and (4) examine implications for ecosystem services and management.

Methods

Study area and ecological site

Field studies were conducted in plots distributed throughout a 1500-km^2 area located on the central Colorado Plateau in southeastern Utah, USA (Fig. 1). Approximately 25% of the study area is located within Canyonlands National Park (CNP), portions of which were grazed by livestock (cattle) from the late 1880s until 1974. The remainder of the study area encompasses the adjacent Indian Creek grazing allotment of the Dugout Ranch, where livestock grazing continues to be the dominant land use. Elevation ranges from 1470 to 2044 m. Ranges of climate variables (from Western Regional Climate Center, ⟨http://www.wrcc.dri.edu⟩, unless otherwise noted) are as follows: (1) mean annual precipitation (MAP), 210 to 255 mm; (2) mean annual temperature, 10.7 to 12.1°C; and (3) the ratio of MAP to potential evapotranspiration, 0.18 to 0.34 (Flint and Flint 2007; 0.20 is defined as the division between arid and semiarid zones, Reynolds and Stafford Smith 2002).

We used the U.S. Department of Agriculture Natural Resources Conservation Service (USDA NRCS) ecological site system as a framework for landscape stratification and ecosystem classification (Herrick et al. 2006, Bestelmeyer et al. 2009). In this system, ecological sites are differentiated by physical attributes including inherent soil properties (texture, depth, and horizonation), geomorphic setting, and climate, and the potential (rather than current) vegetation associated with these physical attributes within a specific ecoregion (Herrick et al. 2006, Bestelmeyer et al. 2009). Despite the term "ecological site," they do not correspond to a particular study site or plot on the landscape but rather to a class of land. In this study, we focused on the Semidesert Sandy Loam (SDSL hereafter) ecological site because of its broad spatial extent and high degree of past and present use for livestock grazing throughout the region. We further restricted our analyses to the Begay soil series (a coarse-loamy, mixed, superactive, mesic Ustic Haplocambid), which is the most common soil attributed to the SDSL site in the region (USDA NRCS 1991). The Begay soil is formed in eolian and alluvial deposits derived from calcareous sandstone and is found in broad valleys and on structural benches with gentle slopes. Surface textures range from fine sandy loams to loamy fine sands, depths range from 100 to over 150 cm, and surface pH is moderately alkaline.

In relatively undisturbed settings, the vascular plant community of the SDSL site is characterized by a mixture of perennial grasses, shrubs, and annual herbaceous species. Common perennial grasses include *Stipa hymenoides* Roemer & Schultes and *S. comata* Trinius & Ruprecht (C_3 bunchgrasses; all nomenclature follows Welsh et al. 2003), *Sporobolus* R. Br. spp. (short-lived C_4 bunchgrasses), and *Hilaria jamesii* (Torrey) Bentham and *Bouteloua gracilis* (Humboldt, Bonpland, & Kunth) Lagasca ex Steudel (rhizomatous C_4 grasses). Common shrubs include *Atriplex canescens* (Pursh) Nuttall and *Krascheninnikovia lanata* (Pursh) Meeuse & Smit (both palatable to livestock and may exceed perennial grasses), as well as the subshrub *Gutierrezia sarothrae* (Pursh) Britton & Rusby (unpalatable to livestock). Common exotic annuals include the invasive C_3 grass *Bromus tectorum* L., the invasive C_4 forbs *Salsola tragus* L. and *S. paulsenii* Litvinov, and the C_3 forb *Erodium cicutarium* (L.) L'Hertier. Biological crust (cyanobacterially dominated but containing lichens such as *Collema* and *Placidium*, and mosses such as *Syntrichia*) is an important functional group associated with the SDSL and many other ecological sites on the Colorado Plateau (Bowker and Belnap 2008, Bowker et al. 2008, Miller 2008).

Plots sampled for this study were classified as never grazed, formerly grazed, or currently grazed based on past or current accessibility and evidence of livestock use. However, the relative intensities of past and current grazing use are highly variable spatially due to deep canyons and high sandstone walls that limit livestock movements and access to forage and water.

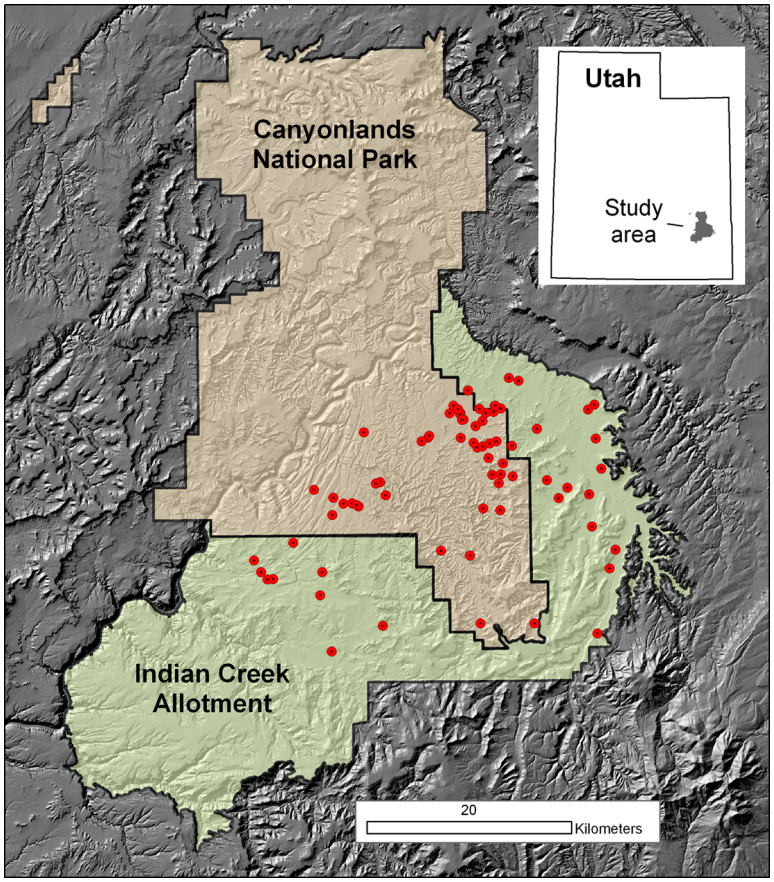

Fig. 1. Map showing the location of the study area in southeastern Utah, USA, and the distribution of plots (points) in Canyonlands National Park and the Indian Creek grazing allotment.

Conceptual model of ecosystem dynamics

We developed an a priori state-and-transition model (STM) describing putative alternative states associated with the SDSL ecological site (Fig. 2). STMs serve to describe alternative states and general processes most likely to have caused state transitions in the past (Westoby et al. 1989). Our model articulates hypotheses about temporal patterns and processes based upon observed patterns of spatial variability. Dynamics and associated processes depicted in the model motivated our selection of particular field measurements, and they provided a framework for our analytical approach. The model asserts the existence of four alternative states (one historical and three extant) and is based on field observations and previous investigations of this ecological site in the study area (Kleiner and Harper 1972, Belnap and Phillips 2001, Neff et al. 2005, Miller et al. 2006, Belnap et al. 2009). States in our conceptual model are differentiated by the relative abundance of generalized functional groups of biota that differ in their effects on ecosystem processes and in their responses to livestock grazing, surface disturbances, and climate. These three generalized groups consist of biological crust, perennial grasses and shrubs, and invasive annual plants. The specific composition of each of these three groups can vary spatially in relation to elevation and subtle soil-geomorphic properties, and temporally in response to climate and disturbance history. We accommodate this degree of natural variability in the model through our generalized characterization of functional groups, thereby ensuring the plausibility that divergent extant states derive from the same initial conditions.

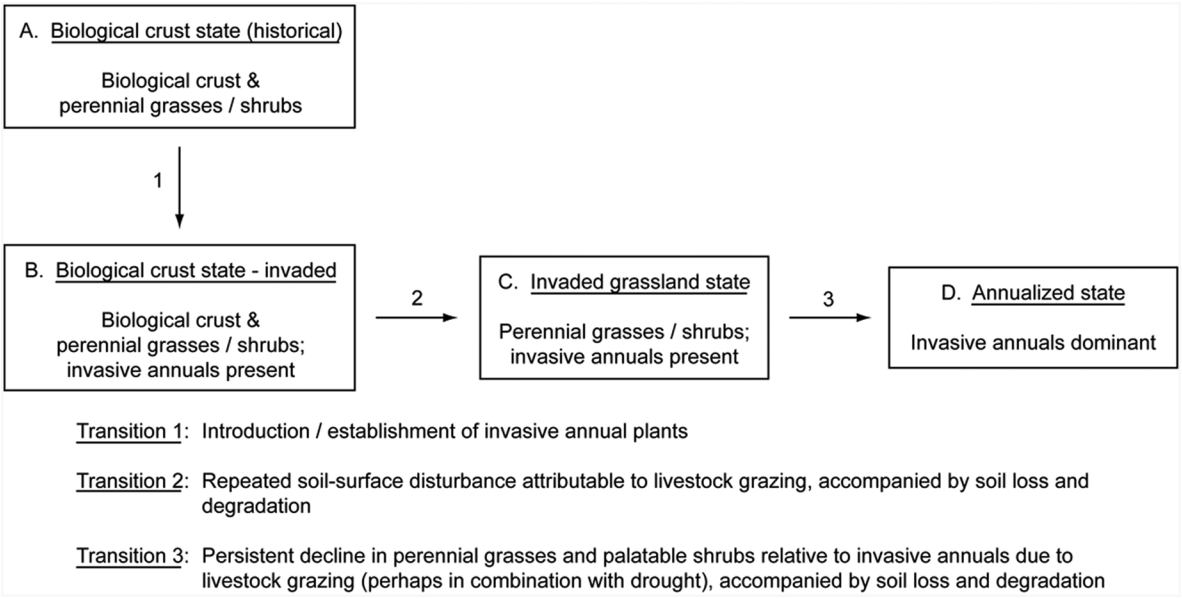

Fig. 2. Conceptual state-and-transition model for the SDSL ecological site. Boxes A–D represent putative alternative states and numbered arrows reflect hypothesized causal processes responsible for persistent transitions among states.

Sampling design

We sampled 72 SDSL plots as part of a larger study of ecological site variability. We used the Generalized Randomized Tessellation Stratification (GRTS) method (Stevens and Olsen 2004) to select spatially balanced sampling locations within strata that consisted of soil map units (excluding units dominated by rock outcrops) delineated by the SSURGO (soil survey geographic database) order-three soil survey (USDA NRCS 1991) for areas inside and outside of CNP, and fenced pastures on the Indian Creek allotment ($n = 48$). The GRTS method minimizes clustering of sampling locations that can occur with simple random sampling. To capture the full range of variability in the SDSL site, we also used targeted sampling to select an additional 24 plot locations. In the field, the ecological site membership of each plot was determined based on soil properties and landscape setting. At each location, a sampling plot consisted of three parallel 50-m transects separated by 25 m and oriented parallel to the hillslope contour. Where initial transect alignments were found to cross soil-geomorphic boundaries separating different ecological sites, plot locations were adjusted objectively to ensure that sampling was restricted to the SDSL ecological site. Sampling was conducted from late May through October in 2006–2008. For all analyses described below, data for GRTS plots and targeted plots were combined in a single data set.

Field measures

Field measures were selected specifically to quantify structural and functional attributes related to the states and processes depicted in our conceptual model.

Biotic composition, ground cover, spatial structure of vegetation, livestock use.—At each plot, live foliar cover of vascular plants and cover of biological crust (differentiated as dark cyanobacteria, moss, or lichen), litter, rocks, and bare ground were estimated by line-point intercept sampling with 1-m sampling intervals (150 points per plot; Herrick et al. 2005). As an indicator of wind-erosion resistance (Okin 2008), gaps between perennial plant canopies were measured using line-intercept sampling following procedures described by Herrick et al. (2005). The frequency of livestock dung was acquired from 1×1 m quadrats placed at 5-m intervals along each transect (30 quadrats per plot). Dung frequency provides an index of

recent but not past livestock use. We also recorded a list of all plant species observed in the plot.

Soil-surface attributes.—As an additional indicator of erosion resistance and soil biotic activity, surface soil aggregate stability was measured using a field-based soil stability kit (Herrick et al. 2001), with plot-level averages based on measurements at six random points per transect (18 subsamples per plot). Several ecological functions of biological crust are attributable to interspace soil-surface roughness associated with well-developed crust communities. Fine-scale soil-surface roughness facilitates the retention of overland water flow (Ward and Trimble 2004), the retention of litter and plant propagules, and the creation of safe sites for seed germination and establishment (Harper et al. 1965). We measured soil roughness in plant interspaces by draping a 20-cm jewelry chain with 2-mm chain links across surface microtopographic features and measuring the horizontal distance between the ends of the chain. Measures were acquired at 10-m intervals along each transect (15 subsamples per plot) and averaged to derive a plot-level mean. A soil roughness index (in percent) was calculated for each plot as

$$\text{Soil Roughness Index} = (1 - L_2/L_1) \times 100$$

where L_2 is the mean horizontal distance in cm and L_1 is the length (20 cm) of the chain (Saleh 1993).

In sandstone-derived soils in our study area, magnetic minerals in soil are attributable to deposits of far-travelled eolian dust that contribute significant amounts of silt, clay, and rock-derived nutrients (Reynolds et al. 2006). As an indicator of dust, soil fines, and rock-derived nutrients, we measured the magnetic susceptibility of the soil surface with a MS-20 magnetic susceptibility (MS) meter (GF Instruments, s.f.o.; Czech Republic) with a sensitivity of 10^{-6} SI units. Measures were acquired at 10-m intervals along each transect (15 subsamples per plot), and averaged to derive a plot-level mean. When compared among sites with similar landscape settings and soils, lower MS readings are interpreted to indicate depletion of eolian silts, clays, and associated soil resources following soil destabilization and wind erosion (Neff et al. 2005, Reynolds et al. 2010). In combination, soil aggregate stability, soil-surface roughness, and MS all are interpreted as relative indicators of soil health (high stability, roughness, and MS) and soil degradation (low stability, roughness, and MS).

Statistical analysis

Cluster analysis.—As an empirical examination of our state-and-transition model we applied a fuzzy cluster analysis (Equihua 1990) to group and classify plots according to their degree of similarity in biophysical attributes. In fuzzy clustering (as opposed to "hard" clustering), observations are assigned membership values for all clusters, where membership values sum to one and cluster identity is determined by the maximum value (Equihua 1990). In ecological applications, this classification approach explicitly acknowledges variability and the fact that samples naturally will differ in their degree of affinity for a given cluster, and may display some affinity for multiple clusters simultaneously (Roberts 1989, Equihua 1990). Fuzzy clusters were derived using four variables as classification criteria and Euclidean distances among plots in NCSS 2001 software (Hintze 2004). This method is compatible only with Euclidean distance; use of this distance measure is justified by approximate normal distributions of data, approximate linear intercorrelation among variables, and few zero values. To facilitate a linkage between our conceptual model and the cluster analysis, we used a parsimonious set of classification variables that was based on the compositional attributes of states depicted in the model. Classification variables included (1) percent cover of biological crust, (2) percent live cover of perennial grasses and palatable shrubs, (3) percent relative live cover of invasive annual plants, and (4) percent cover of bare ground. We used principal components analysis (PCA) to visualize and describe underlying differences among clusters in terms of the four classification variables. PCA was conducted using PC-ORD 5.0 (McCune and Mefford 2006).

Patterns among and within clusters.—To characterize clusters quantitatively and interpret them with respect to states outlined in the STM, we conducted multivariate and univariate analyses on a suite of 26 variables. We used univariate analysis of variance (ANOVA), or Kruskal-Wallis

tests when the assumptions of normality were not met, to determine which specific measurements differed among clusters. Contrasts were performed using the Tukey HSD test.

To determine if samples within clusters were distinguishable based upon grazing status, we conducted a multi-response permutation procedure (MRPP) of currently and historically grazed plots within the *grass-bare* and *annualized-bare* clusters; because only two *biocrust* plots were currently grazed, an MRPP analysis of grazing status was not conducted for the *biocrust* cluster. (Cluster names are described in Results.) MRPP uses distance measures (Euclidean in our case, for consistency with other techniques) and randomization tests to determine if groups are different. It calculates chance corrected within-group agreement (A, ranging from 0–1, with values >0.1 often considered to indicate a strong degree of agreement within groups). MRPP was conducted in PC-ORD 5.0 (McCune and Mefford 2006).

To determine if individual variables differed by grazing status within cluster assignments, we used a two-way mixed-effects ANOVA with cluster assignment, grazing status, and cluster × grazing as fixed effects, and year as a random effect. Year was included to control for differences in annual precipitation among the years of field sampling. Because the ANOVA was unbalanced (due to unequal sample sizes among fixed and random effects), the restricted maximum likelihood approach was used to estimate parameters (Spilke et al. 2005). In the *biocrust* cluster all but two plots were classified as never or as formerly grazed. Because this prohibits investigating interactive effects of cluster assignment and grazing status, data from the *biocrust* cluster were omitted from the analysis. The mixed-effects models were conducted in SAS 9.2 (Littell et al. 2006).

Simulation modeling

We used a wind erosion model (WEMO hereafter) to investigate effects of measured biophysical attributes on predicted rates of wind-driven soil movement at our plots (Okin 2008). WEMO predicts horizontal dust flux ($g \cdot cm^{-1} \cdot d^{-1}$) on the basis of wind velocity, plant height, the size-class distribution of gaps between plant canopies, total plant cover, threshold shear velocity (TSV; Gillette et al. 1982), and a suite of other variables. TSV is the surface wind velocity required to initiate soil movement and thus is a measure of soil erodibility. Direct measurement of TSV requires a wind tunnel or similar apparatus. For our plots, we estimated TSV from soil aggregate stability measures using data from wind tunnel observations on soils similar to those of the SDSL ecological site (J. Belnap, *unpublished data*). In the wind tunnel data, TSV variability increased with increasing soil aggregate stability, and residuals were not normally distributed around a least-squares model. Therefore, we used quantile regression to fit separate linear models through the 10th, 50th, and 90th percentiles of the empirical TSV data (Cade and Noon 2003). Here we report WEMO predictions based on the 10th percentile model because fluxes predicted with this model were most consistent with flux observations from a continuous monitoring effort (since 1999) at two of our plots (VP and NR in Belnap et al. 2009). The rate of wind erosion is proportional to the cube of wind velocity above TSV (Bagnold 1941), so we used a range of wind velocities (17.5, 26.25, and 35.0 m/s, measured at 10 m above the surface) in WEMO to examine relative increases in predicted dust fluxes with increasing wind velocity. The highest velocity value we used corresponds to the maximum wind velocity reported in the study-area region (Williams et al. 1995). We used perennial plants only as the basis for WEMO inputs for canopy gaps, plant cover, and plant height because production and cover of annual plants are highly responsive to precipitation variability and contribute little to erosion resistance during periods of drought (Belnap et al. 2009). Thus predicted dust fluxes represent relative measures of susceptibility to wind erosion during drought.

Results

Cluster analysis

Fuzzy cluster analysis resulted in three clusters with minimized within-cluster variance and maximized among-cluster variance. Short-hand notation for clusters used hereafter are *biocrust* (biological crust, perennial grasses, and palatable shrubs), *grass-bare* (perennial grasses and bare ground), and *annualized-bare* (invasive annual

grasses or forbs, and bare ground); these clusters correspond well with states B, C, and D, respectively, in the STM (Fig. 2). PCA results illustrate how the three clusters differed on the basis of the four classification variables (Fig. 3). The *biocrust* cluster contained 21 plots, the *grass-bare* cluster contained 24 plots, and the *annualized-bare* cluster contained 27 plots. Table A1 (Appendix) summarizes the sample numbers by year, water-year precipitation, cluster, and grazing status.

ANOVA results highlighted numerous distinguishing characteristics of each cluster. Of the 26 variables considered, only perennial forb cover and unpalatable shrub cover did not differ between at least two clusters (Table 1). The *biocrust* cluster was characterized by 5.3 times greater biological crust cover than the *grass-bare* cluster and 7.9 times greater crust cover than the *annualized-bare* cluster. As a result, averages for soil aggregate stability, soil surface roughness, and magnetic susceptibility also were highest in the *biocrust* cluster. The *grass-bare* cluster did not differ strongly from the *biocrust* cluster in terms of the perennial plant community (with the exception of less palatable shrub cover), but bare ground in the *grass-bare* cluster was 2.6 times greater than the *biocrust* cluster. Cover of native annual forbs in the *grass-bare* cluster was only 28% of that found in the *biocrust* cluster. Bare ground in the *annualized-bare* cluster was two times greater than in the *biocrust* cluster. Average relative cover of invasive exotic annuals in the *annualized-bare* cluster was five times greater than in the *biocrust* cluster and 7.7 times greater than in the *grass-bare* cluster; the *annualized-bare* cluster also was characterized by higher litter cover than the *grass-bare* cluster. Average total live cover of all vascular plants in the *biocrust* cluster was twice the average found in the *grass-bare* cluster. Both richness and total live cover of all functional groups (including biological crust) in the *biocrust* cluster were significantly higher than in the other two clusters. Average vascular plant richness in the *biocrust* cluster tended to be greater than in the *grass-bare* cluster and was significantly higher than in the *annualized-bare* cluster. Additional differences among clusters are presented in Table 1.

Empirical patterns within clusters

MRPP indicated that formerly grazed and currently grazed groups within the *annualized-bare* cluster ($A = 0.24$, $P < 0.0001$) and the *grass-bare* cluster ($A = 0.04$, $P = 0.015$) differed overall. Within the *grass-bare* and *annualized-bare* clusters, ANOVA revealed that grazing status (currently versus formerly grazed) was statistically significant for seven of 26 variables (Table 2 and Appendix: Table A2). Compared to currently grazed *grass-bare* plots, formerly grazed *grass-bare* plots were characterized by greater abundance of biological crusts as well as greater magnetic susceptibility and surface roughness—both of which are functionally related to biological crust cover. Currently and formerly grazed *annualized-bare* plots primarily differed in higher relative abundance of exotic grasses and forbs, respectively. This difference may be partially accounted for by a difference in elevation among these groups, as formerly grazed *annualized-bare* plots were lower and drier.

Predicted levels of wind erosion

Predicted levels of wind erosion differed among and within clusters as a function of soil stability and vegetation structure (Fig. 4; Appendix: Table A3). For the *biocrust* cluster, no erosion (zero flux) was predicted by WEMO except at the maximum wind velocity for two plots with relatively low soil aggregate stability values (4.8 and 4.9, compared with cluster mean 5.5; Appendix: Table A3) and thus relatively high wind erodibility. In the *grass-bare* cluster, higher average levels and greater frequency (percentage of plots with flux) of wind erosion were predicted for currently grazed plots than for formerly grazed plots with significantly higher levels of biological crust. Predicted erosion frequency in currently grazed plots in the *grass-bare* cluster also tended to be greater than in currently or formerly grazed plots in the *annualized-bare* cluster at all three wind velocities (Appendix: Table A3). At intermediate and maximum wind velocities, formerly grazed plots in the *annualized-bare* cluster were predicted to have the highest average levels of wind erosion, with maximum fluxes predicted for a plot with a median gap size of 2153 cm and soil aggregate stability value of 3.3 (Fig. 4; Appendix: Table A3). In contrast, no wind erosion was predicted for a

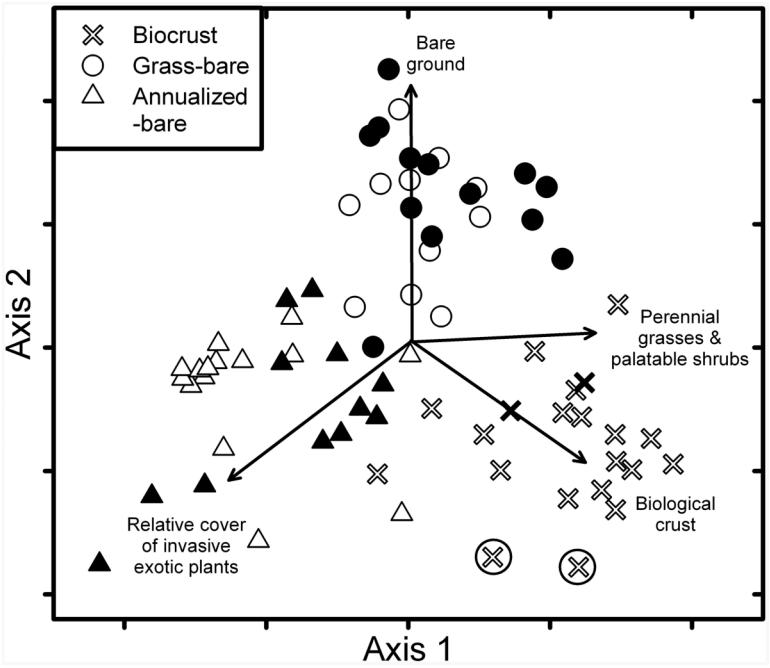

Fig. 3. PCA ordination of plots based on the four classification variables used in the fuzzy cluster analysis. Clusters are noted as *biocrust*, *grass-bare*, and *annualized-bare*. These clusters closely match states B, C, and D, respectively in Fig. 1. For each cluster symbol, closed symbols indicate plots that are currently accessible to grazing, open symbols indicate plots that formerly were grazed, and circled open symbols indicate two plots that were never grazed. Vectors indicate loadings of four classification variables on the two axes. Axis 1 accounts for 42.6% of the variability and is most highly correlated with relative cover of invasive exotics ($r = -0.85$), cover of perennial grasses and palatable shrubs ($r = 0.70$), and cover of biological crust ($r = 0.69$). Axis 2 accounts for 36.2% of the variability and is most highly correlated with bare ground ($r = 0.97$).

plot in the *biocrust* cluster that also was characterized by large canopy gaps (median gap size 1885 cm) but that had a higher soil aggregate stability value of 5.2 (Fig. 4).

Discussion

Empirical evidence for alternative states

Our empirical results document the existence of alternative states defined by significant differences in functional group structure for the SDSL grassland ecosystem (Fig. 5). Our analysis substitutes space for time, and we infer that states represented by the *grass-bare* and *annualized-bare* clusters reflect persistent changes in ecosystem structure and function triggered by interactions of livestock grazing (reduction of perennial grasses and palatable shrubs through selective herbivory), associated soil disturbances (depletion of soil resources through trampling, loss of biological crust, soil destabilization, and accelerated erosion), and climate (drought-induced reduction in grazing tolerance of preferred forage species) (Fig. 2). The fact that *grass-bare* and *annualized-bare* plots in CNP have been protected from livestock impacts for more than 30 years strongly suggests that the striking among-cluster differences in structure (Fig. 3) and function (Fig. 4) can be persistent for at least multiple decades and are effectively irreversible at a time scale relevant to current management without costly investments in ecological restoration. Among-cluster differences in WEMO results are consistent with patterns in magnetic susceptibility, which was significantly higher in the *biocrust* cluster than in *grass-bare* and *annualized-bare* clusters—suggesting greater wind erosion and soil depletion in these two clusters. These results also support and expand upon other recent research that has examined legacy effects

Table 1. Means (standard errors) of 26 variables for three fuzzy clusters, and ANOVA results.

Variables	Biocrust	Grass-bare	Annualized-bare
Biological crust (cover %)	34.1^{A} (3.0)	6.4^{B} (1.4)	4.3^{B} (1.0)
Perennial grasses and palatable shrubs (cover %)	20.6^{A} (2.8)	14.9^{A} (2.0)	11.4^{B} (2.0)
Relative cover of invasive exotic annuals (%)	11.7^{A} (2.7)	7.7^{A} (1.5)	59.3^{B} (3.9)
Bare ground (cover %)	18.7^{A} (1.7)	48.6^{B} (2.0)	36.6^{C} (3.3)
Annual grasses, native (cover %)	2.6^{A} (0.6)	1.3^{A} (0.4)	0.1^{B} (0.04)
Annual grasses, exotic (cover %)	4.9^{AB} (1.7)	0.6^{B} (0.2)	13.1^{A} (3.2)
Annual forbs, native (cover %)	16.7^{A} (3.6)	4.7^{B} (1.2)	5.1^{B} (1.6)
Annual forbs, exotic (cover %)	1.1^{A} (0.5)	1.4^{A} (0.5)	9.2^{B} (1.6)
Perennial forbs (cover %)	1.4^{A} (0.6)	1.5^{A} (0.7)	0.5^{A} (0.1)
Bunchgrasses C_3 (cover %)	3.7^{A} (1.3)	2.5^{A} (0.7)	0.6^{B} (0.3)
Bunchgrasses C_4 (cover %)	3.2^{A} (1.0)	3.1^{A} (1.3)	6.0^{B} (1.3)
Rhizomatous grasses C_4 (cover %)	4.6^{A} (0.8)	5.2^{A} (1.0)	2.4^{B} (0.9)
Palatable shrubs (cover %)	5.5^{A} (0.9)	1.2^{B} (0.5)	1.1^{B} (0.4)
Unpalatable shrubs (cover %)	2.3^{A} (0.7)	1.5^{A} (0.5)	0.9^{A} (0.3)
Total live cover, perennial plants (%)	20.7^{A} (2.8)	14.9^{A} (1.9)	11.4^{B} (1.9)
Total live cover, vascular plants (%)	46.0^{A} (4.6)	22.9^{B} (2.9)	38.9^{A} (3.6)
Total live cover, all functional groups (%)	80.1^{A} (4.8)	29.3^{B} (2.6)	43.3^{C} (4.1)
Functional group richness (no. of functional groups)	8.3^{A} (0.3)	7.0^{B} (0.3)	6.2^{C} (0.3)
Species richness (no. of vascular plant species)	23^{A} (1.4)	19.4^{A} (1.3)	16.7^{B} (1.2)
Soil aggregate stability (index)	5.5^{A} (0.1)	3.8^{B} (0.2)	4.3^{B} (0.2)
Soil surface roughness (index)	11.9^{A} (0.7)	4.8^{B} (0.6)	4.5^{B} (0.6)
Litter (cover %)	49.7^{A} (2.5)	28.4^{B} (1.9)	42.7^{A} (3.4)
Magnetic susceptibility (10^{-6} SI units)	0.18^{A} (0.0)	0.10^{B} (0.0)	0.12^{B} (0.0)
Median size of perennial canopy gaps (cm)	165.9^{AB} (86.2)	78.3^{A} (6.5)	253.7^{B} (83.8)
Elevation (m)	1670.1^{A} (72.1)	1557.1^{B} (114.7)	1623.9^{B} (152.3)
Livestock dung (% frequency)	1.0^{A} (3.6)	11.3^{B} (3.4)	13.3^{B} (3.2)

Notes: Means superscripted with different letters are statistically different at the $\alpha = 0.05$ level using the Tukey HSD test. The first four variables are the classification criteria used to generate clusters.

Table 2. Means (standard errors) of variables by grazing status for the *grass-bare* and *annualized-bare* clusters.

	Grass-bare		Annualized-bare	
Variables	Currently grazed (n=13)	Formerly grazed (n=11)	Currently grazed (n=12)	Formerly grazed (n=15)
Biological crust (cover %)	**2.8 (1.4)**	**10.7 (1.9)**	4.5 (1.4)	4.2 (1.5)
Perennial grasses and palatable shrubs (cover %)	19.6 (3.0)	9.4 (1.3)	15.8 (2.8)	8.0 (2.5)
Relative cover of invasive exotic annuals (%)	7.0 (1.9)	8.5 (2.4)	54.6 (6)	63.1 (5.1)
Bare ground (cover %)	48.8 (3.0)	48.4 (2.8)	29.7 (3.8)	42.1 (4.7)
Annual grasses, native (cover %)	2.0 (0.5)	0.5 (0.3)	0.2 (0.1)	0.1 (0.1)
Annual grasses, exotic (cover %)	0.8 (0.2)	0.4 (0.2)	**23.7 (4.3)**	**4.6 (3.3)**
Annual forbs, native (cover %)	3.6 (0.8)	5.9 (2.5)	2.8 (0.9)	6.9 (2.7)
Annual forbs, exotic (cover %)	1.0 (0.5)	1.8 (0.9)	**1.6 (0.6)**	**15.3 (1.6)**
Bunchgrasses C_3 (cover %)	4.0 (1.1)	0.7 (0.3)	1.1 (0.6)	0.2 (0.1)
Bunchgrasses C_4 (cover %)	5.2 (2.2)	0.5 (0.2)	8.7 (2.3)	3.9 (1.2)
Rhizomatous grasses C_4 (cover %)	5.1 (1.5)	5.3 (1.4)	2.1 (0.9)	2.6 (1.5)
Palatable shrubs (cover %)	0.8 (0.3)	1.6 (1)	1.8 (0.8)	0.4 (0.2)
Unpalatable shrubs (cover %)	2.4 (0.9)	0.3 (0.1)	1.6 (0.6)	0.2 (0.1)
Total live cover, perennial plants (%)	19.6 (6)	9.4 (1.3)	15.8 (2.8)	7.9 (2.5)
Total live cover, vascular plants (%)	27.0 (3.8)	17.9 (4.3)	44.1 (4.3)	34.9 (5.4)
Total live cover, all functional groups (%)	29.8 (3.6)	28.7 (4)	48.5 (4.3)	39.1 (6.5)
Functional group richness (no. of groups)	7.6 (0.2)	6.4 (0.4)	7.0 (0.4)	5.5 (0.5)
Species richness (no. of vascular plant species)	22.1 (2.0)	16.3 (1.8)	19.1 (1.6)	14.8 (1.1)
Soil aggregate stability (index)	3.2 (0.3)	4.4 (0.2)	4.5 (0.3)	4.1 (0.2)
Soil surface roughness (index)	**4.1 (0.6)**	**5.6 (0.5)**	6.2 (0.7)	3.2 (0.7)
Litter (cover %)	28.4 (3.0)	28.4 (2.5)	48.1 (5.2)	38.4 (4.4)
Magnetic susceptibility (10^{-6} SI units)	**0.085 (0.010)**	**0.118 (0.012)**	0.150 (0.015)	0.093 (0.001)
Median size of perennial canopy gaps (cm)	65.0 (6.7)	94.0 (10)	87.1 (9.6)	387.1 (143.4)
Elevation (m)	1566.4 (41.1)	1546.2 (18.1)	**1752.4 (41.9)**	**1521.1 (8.2)**
Livestock dung (% frequency)	**18.5 (4.6)**	**2.7 (2.1)**	**29.7 (7.5)**	**0.2 (0.2)**

Notes: Values in boldface indicate $P < 0.05$, based on two-way mixed-effects ANOVA models with year as a random effect block. Exact P values are in Appendix: Table A2.

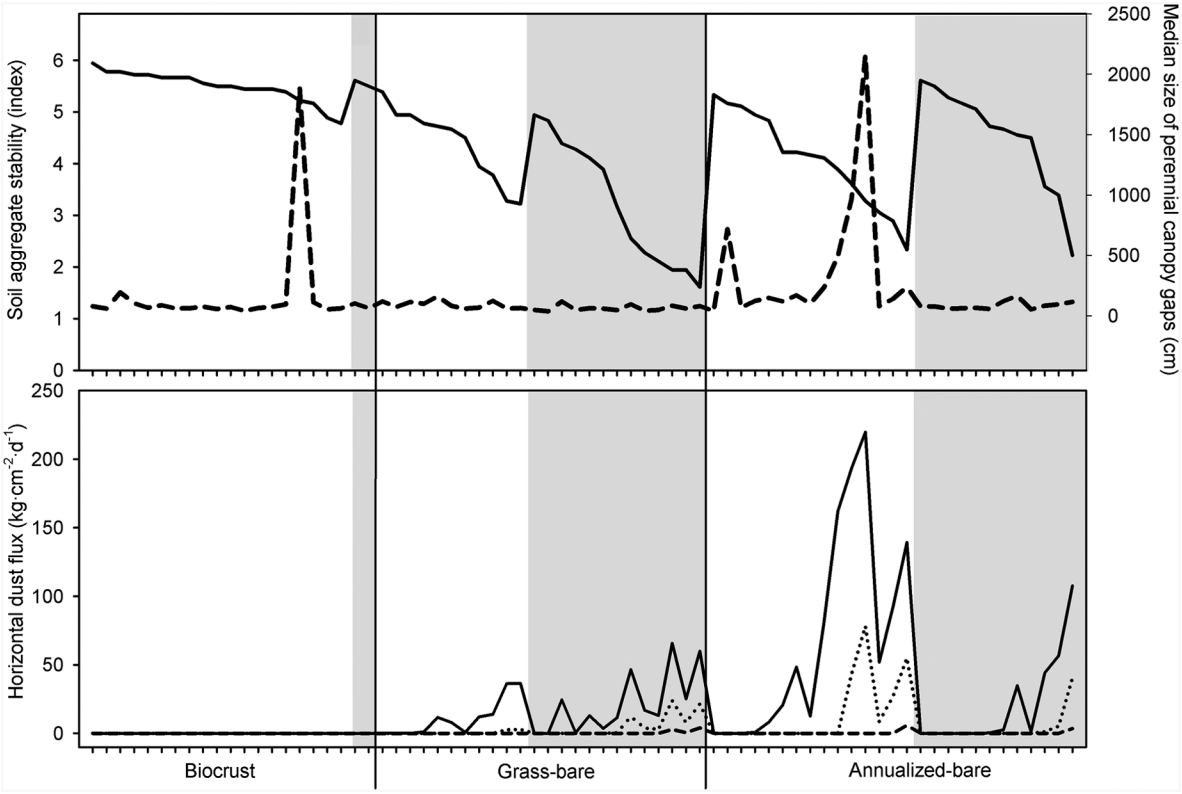

Fig. 4. Soil aggregate stability (top panel, solid line), median gap size between perennial plant canopies (top panel, dashed line), and predicted rates of wind erosion (horizontal dust flux) at three wind velocities (bottom panel; dashed line = 17.5 m/s, dotted line = 26.25 m/s, solid line = 35.0 m/s) for plots categorized by cluster and grazing status (shading indicates plots currently accessible to grazing). Within each cluster and grazing category, plots are ordered from left to right by decreasing soil aggregate stability. Data are discrete points, indicated by tick marks on the X axis, but are represented as lines for easier viewing.

of livestock grazing on soil biogeochemical properties and erosional processes in our study area (Neff et al. 2005, Belnap et al. 2009).

The *biocrust* and *grass-bare* states differed significantly with respect to biological crust cover and related soil attributes. But these differences were not accompanied by differences in perennial grass cover and composition despite our interpretation that lower measures of soil aggregate stability, surface roughness, and MS were indicative of degraded soil conditions in the *grass-bare* state relative to the *biocrust* state. In terms of the vascular plant community, evidence for consequences of soil differences may be reflected in the much higher cover of native annual forbs in the *biocrust* state (16.7%) versus the *grass-bare* state (4.7%, Table 1). This pattern could be attributable to greater retention of propagules and availability of safe sites in roughened interspaces dominated by biological crust, as well as to greater resource availability to seedlings in undisturbed interspaces that retain higher levels of eolian fines. This hypothesis is consistent with data linking fine-scale patterns in MS and eolian fines to distributional patterns of annual plants including the exotic *Bromus tectorum* (Reynolds et al. 2010). In the *grass-bare* state, formerly grazed plots had higher measures of biological crust cover, surface roughness, and MS (Table 2) relative to currently grazed plots, suggesting some recovery of soil attributes following 30 years of rest from livestock disturbance.

In the *grass-bare* and *annualized-bare* states, there was an unexpected tendency for currently grazed plots in the Indian Creek allotment to

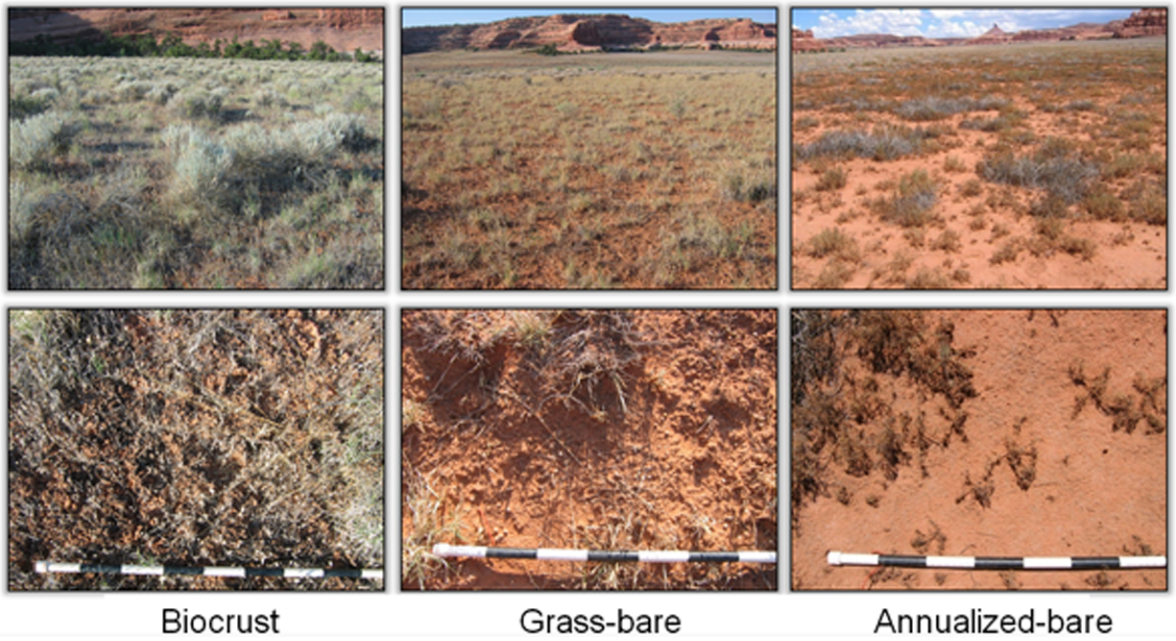

Fig. 5. Example photos from plots classified into three clusters representing ecosystem states *biocrust* (left), *grass-bare* (middle), and *annualized-bare* (right) within the SDSL ecological site. Top photos show general vegetation characteristics. Bottom photos show soil-surface characteristics including differences in roughness and in the relative abundance of biological crust and bare ground.

have higher cover of perennial grasses than formerly grazed plots in CNP (Table 2), suggesting potential facilitation of grass establishment by recent livestock disturbance. Instead, we interpret this pattern primarily as an artifact of sampling year precipitation conditions. Combining both states, 19 of 26 (73%) formerly grazed plots in CNP were sampled in the dry year of 2006 (Appendix: Table A1), whereas 21 of 25 (84%) of currently grazed plots in the Indian Creek allotment were sampled in comparatively wet years of 2007 and 2008 that were more favorable for grass establishment and growth.

Relation to resilience theory

Functional group structure is recognized as the key biotic control of ecosystem resilience and sustainability (Chapin et al. 1996). This case study is unique for its incorporation of the biological crust functional group in an alternative state framework and for its documentation of a state characterized by high areal coverage of biological crust relative to vascular plants. Though underreported, the current or former existence of such a state is widespread among many forms of dryland ecosystems (Bowker and Belnap 2008, Bowker et al. 2008, Miller 2008), including at least five of the eight most common ecological sites sampled in our study area in conjunction with the current study (M. E. Miller, *unpublished data*). Biological crust effects on soil stability, nutrient cycling, hydrologic processes, and vascular plant establishment indicate a need for explicit consideration of this functional group in ecosystem analyses and management, particularly in systems characterized by a high degree of biological crust coverage and functionality relative to the vascular plant community.

Resilience is promoted both by redundancy in the performance of key ecosystem functions and by diversity in biotic responses to perturbations (Walker 1992, Walker et al. 1999, Elmqvist et al. 2003). These principles are well-illustrated by the biological crust functional group and *biocrust* cluster in our case study. Sparsely vegetated drylands with high coverage of biological crust lack redundancy with respect to ecosystem functions performed by the crust functional

group. In such systems, key functions including the capture and retention of mobile soil resources and the mediation of vascular plant establishment are effectively lost from interspaces when biological crust is lost from the system. The likelihood that high-functioning biological crust will be eliminated from a system by surface disturbance (as evidenced by the *grass-bare* and *annualized-bare* clusters) is heightened by the fact that most biological crust components and functions tend to recover slowly or not at all following extensive surface disturbance and destabilization (Belnap and Eldridge 2003). Thus as a functional group, biological crust generally lacks diversity in its responses to surface disturbance—perhaps the most ubiquitous human impact on drylands.

Implications for ecosystem services and management

Dryland degradation is widely recognized as having a biophysical component (reflecting reductions in soil resources, biological diversity, or other ecosystem attributes) as well as a socioeconomic component (reflecting reductions in the valued services that society derives from ecosystems) (Reynolds and Stafford Smith 2002, Reynolds et al. 2007). Biophysical state changes described here may or may not be recognized as socioeconomic degradation, depending on societal perceptions of how such changes affect services that are most highly valued (Reynolds and Stafford Smith 2002, Walker et al. 2002). Of the 6000 ha of SDSL in the currently grazed Indian Creek allotment, we estimate that 15% (900 ha) is in *biocrust* condition, whereas 50 and 35% are in *grass-bare* and *annualized-bare* condition, respectively. Of the 4500 ha of SDSL in CNP, we estimate that 45% (2025 ha) is in *biocrust* condition, with 21 and 34% in *grass-bare* and *annualized-bare* condition, respectively. Together, these proportions can be viewed as comprising an investment portfolio of ecosystem goods and services because each state has distinct biophysical attributes that have the potential to support distinct sets of socioeconomic values. Investment in a particular state, and therefore in a particular set of goods and services, may result in trade-offs and synergies relative to other goods and services.

The SDSL ecological site, like many drylands worldwide, by tradition has been valued primarily for its provision of livestock forage in support of the livelihoods and cultural traditions of local residents. With respect to total perennial livestock forage, the *biocrust* and *grass-bare* clusters both appear to exhibit greater value than the *annualized-bare* cluster (Table 1). Yet maintenance of the *biocrust* state requires that surface disturbances be limited, thereby greatly constraining access to available forage and potentially reducing the perceived value of this state relative to states with greater forage accessibility. Thus, an investment portfolio emphasizing livestock forage favors a landscape dominated by the *grass-bare* state.

Increasingly, drylands are recognized as providing a suite of ecosystem services (Havstad et al. 2007), and investment in one may incur trade-offs with others either in space or time (Rodríguez et al. 2006). For example, use of forage for livestock production has the potential to incur costs in terms of diminished erosion resistance. In this case study, SDSL clusters clearly differed with respect to modeled levels of wind erosion, with the *biocrust* cluster emitting essentially no dust, the *grass-bare* cluster consistently emitting dust, and the *annualized-bare* cluster potentially becoming a major dust source when drought conditions limit cover of annual plants. Dust emissions from unstable drylands can have downwind consequences through effects on ecosystem biogeochemistry (Neff et al. 2008), mountain snowpack and downstream water delivery (Painter et al. 2010), air quality and human health, and atmospheric dust concentrations that can affect the global energy balance (Field et al. 2010). Economic costs of these downwind consequences are potentially great but rarely considered in local decision making where management for dust abatement is at odds with maximizing livestock production.

Carbon (C) storage is another ecosystem service with increasing importance in the context of climate change mitigation efforts, and represents another service compromised by investment in pastoralism. Data for total live cover plus litter (Table 1) approximate relative C stocks for the three SDSL clusters. The *biocrust* cluster emerges as clearly superior in this way, supporting the greatest average cover of vascular plants, biological crust, litter, and their sum (130% total).

Although the *annualized-bare* cluster also may support high total live cover plus litter (86% total), live cover and litter both fluctuate greatly in response to precipitation due to dominance by annual plants. The *grass-bare* state appears to be the most depauperate in terms of C-storage potential (58% total), although the *annualized-bare* cluster likely would be lower during drought years. Neff et al. (2005) demonstrated a 60–70% difference in soil C between plots in *biocrust* condition and plots in *grass-bare* condition in our study area, and Barger et al. (2006) documented significant C loss with surface disturbance of plots in *biocrust* condition.

In addition to trade-offs, synergies may emerge when managing for multiple outcomes. For example, there is no conflict between management emphasizing dust abatement and C storage; if management actions are taken to enhance one, the other is likely to be enhanced as well. Other non-traditional valuations of ecosystem states include biological diversity, a supporting service which ensures long-term sustainability of forage and other values (Chapin et al. 2009, Stafford Smith et al. 2009). In terms of biodiversity, we found *biocrust* > *grass-bare* > *annualized-bare* in functional group and species richness, indicating another synergy with C storage and dust abatement.

Future strategies for ecosystem management would benefit from explicit evaluation of existing ecosystem states, the breadth of ecosystem services that each can support, and potential risks, trade-offs, and synergies associated with alternative management strategies. Applying such an approach to the SDSL ecological site examined in our study could result in a range of different management prescriptions that also could change over time in response to ever-shifting valuations of costs and benefits due to climate change, for example. Canyonlands National Park currently is invested primarily in a portfolio emphasizing biodiversity, C storage, and dust abatement provided by the *biocrust* state, but the legacy of past disturbance remains apparent in the high coverage of the *annualized-bare* state. Because grazing is no longer permitted in CNP, the *annualized-bare* state has little economic value. Active restoration of *annualized-bare* areas is warranted to attain states with higher functional diversity to enhance resiliency to climate change and drought, as well as to enhance long-term capacity for C storage, dust control, and biodiversity conservation. In the case of the Indian Creek allotment, where the current portfolio favors the provision of livestock forage, lands in *annualized-bare* condition might continue to be grazed only if analysis indicates that benefits for livestock production exceed costs attributable to dust emissions and diminished capacity for C storage and biodiversity conservation. Likewise, where benefits exceed costs, lands in *grass-bare* condition might be managed for livestock production but in a careful manner that minimizes risks of dust emissions and enhances resilience to mitigate risks of further degradation to the *annualized-bare* state. If the balance of the cost-benefit calculus changes, then these lands might be retired or rested from grazing, or actively restored. Acknowledging the interplay between alternative ecosystem states and economic forces will illuminate management strategies which maximize the provision of ecosystem goods and services.

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APPENDIX

Additional results

Table A1. Water-year precipitation at a long-term weather station in the study area (elevation 1537 m), and numbers of plots by year and grazing status within the *biocrust*, *grass-bare*, and *annualized-bare* clusters.

	Water-year precipitation		Biocrust	Grass-bare		Annualized-bare	
Year	mm	% of MAP	Never or formerly grazed	Currently grazed	Formerly grazed	Currently grazed	Formerly grazed
2006	167	77.6	3	4	9	0	10
2007	283	132.1	10	7	1	2	3
2008	239	111.1	8	2	1	10	2

Note: MAP is mean annual precipitation.

Table A2. *P* values for main and interactive effects of cluster assignment and grazing status for the *grass-bare* and *annualized-bare* clusters, based on two-way mixed-effects ANOVA models with year as a random effect block.

Variables	Effect		
	Cluster	Grazing	Cluster × grazing
Biological crust (cover %)	0.167	**0.004**	**0.001**
Perennial grasses and palatable shrubs (cover %)	**0.001**	0.393	0.405
Relative cover of invasive exotic annuals (%)	**<0.001**	0.236	0.573
Bare ground (cover %)	**0.040**	0.219	0.137
Annual grasses, native (cover %)	**<0.001**	0.654	0.117
Annual grasses, exotic (cover %)	**0.016**	**0.010**	**<0.001**
Annual forbs, native (cover %)	0.647	0.037	0.885
Annual forbs, exotic (cover %)	**<0.001**	**<0.001**	**0.002**
Bunchgrasses C_3 (cover %)	**0.001**	0.286	0.372
Bunchgrasses C_4 (cover %)	**0.001**	**0.002**	0.393
Rhizomatous grasses C_4 (cover %)	**0.002**	0.328	0.563
Palatable shrubs (cover %)	0.634	0.316	0.977
Unpalatable shrubs (cover %)	0.133	**<0.001**	0.485
Total live cover, perennial plants (%)	**0.001**	0.393	0.405
Total live cover, vascular plants (%)	**<0.001**	0.085	0.480
Total live cover, all functional groups (%)	0.061	0.069	0.237
Functional group richness (no. of groups)	**0.011**	0.156	0.627
Species richness (no. of vascular plant species)	**0.011**	0.706	0.289
Soil aggregate stability (index)	0.565	**0.038**	0.070
Soil surface roughness (index)	**0.035**	0.060	**0.004**
Litter (cover %)	**0.005**	0.814	0.386
Magnetic susceptibility (10^{-6} SI units)	0.328	0.282	**0.025**
Median size of perennial canopy gaps (cm)	**<0.001**	0.109	0.855
Elevation (m)	0.164	**0.025**	**0.001**
Livestock dung (% frequency)	0.800	**<0.001**	**0.046**

Notes: P values less than 0.05 are in boldface. Means are in Table 2 in main text.

Table A3. Descriptive statistics for predicted rates of wind erosion (horizontal dust flux) at three wind velocities in plots categorized by cluster and grazing status.

Cluster	Grazing status (n plots)	Flux statistic	Wind velocity (m/s at 10-m height)		
			17.5	26.25	35.0
Biocrust	Never or formerly grazed (21)	Frequency (%)	0.0	0.0	9.5
		Mean	0.0	0.0	0.4
		CV	0.0	0.0	450.2
Grass-bare	Formerly grazed (11)	Frequency (%)	0.0	18.2	81.8
		Mean	0.0	494.2	10,939.7
		CV	0.0	222.8	124.7
	Currently grazed (13)	Frequency (%)	38.5	53.8	100.0
		Mean	558.8	5571.6	21,527.6
		CV	231.2	151.7	104.3
Annualized-bare	Formerly grazed (15)	Frequency (%)	6.7	33.3	86.7
		Mean	388.4	14,120.6	68,711.5
		CV	387.3	177.5	111.0
	Currently grazed (12)	Frequency (%)	8.3	25.0	58.3
		Mean	292.9	3897.6	20,604.4
		CV	346.4	297.5	166.0

Notes: Frequency indicates the percentage of plots with predicted fluxes greater than zero. Mean flux values are in $g \cdot cm^{-1} \cdot d^{-1}$. CV = coefficient of variation.